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EARTHWORM BIOLOGY AND SOIL FERTILITY

by

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It is 121 years since Darwin (1837) wrote his first paper on the effects of earthworm activity but, despite the voluminous literature which has accumulated since, the importance of earthworms in agricultural soils is still open to question. This review refers to the more important papers in this subject and suggests points on which further research might be profitable. Earthworm populations; their feeding and casting behaviour; their effects on soil structure and chemistry; their influence on crop yields; and the extent to which they are affected by agricultural practice are discussed.

POPULATIONS

There are two major difficulties in estimating earthworm populations. Firstly, the distribution of earthworms is usually irregular and aggregated (Guild, 1952a, b; Satchell, 1955a; Svendsen, 1957a, b) so that estimates are subject to high errors unless large numbers of samples are taken. Consequently, estimates based on samples of a few square yards and expressed in terms of numbers of earthworms per acre may be misleading. Secondly, although chemical expellents (Eaton & Chandler, 1942; Evans & Guild, 1947), electrical methods (Johnstone-Wallace, 1937; Doeksen, 1950; Satchell, 1955b), sieving (Wilcke, 1955), and hand sorting (Bretscher, 1896, Svendsen, 1955) have been used in sampling, none of these methods can be relied upon to recover all the earthworms present in the soil, and the efficiency of the recovery is difficult to assess.

Population densities up to about ½ million per acre have been recorded by Evans & Guild (1947, 1948b) and Guild (1948, 1951), using potassium-permanganate solutions as an expellent, and by Jefferson (1955) using mowrah meal, but these figures appear to be too low since populations of 1¼-3 millions per acre have been recorded in Britain by seven other authors who used different sampling techniques (Edwards, 1929; Ford, 1935; Low, 1955; Reynoldson, 1955; Reynoldson *et al*, 1955; Satchell, 1955a; Svendsen, 1955). Population estimates within the same range have been obtained in Austria (Franz, 1950), Belgium (Van der Drift, 1950), Denmark (Bornebusch, 1930), France (Galoux, 1953; Saussey, 1955), Germany (Dreidax, 1931; Kollmannsperger, 1934; Ronde, 1951, 1953a, b, 1954; Finck, 1952; Graff, 1953; Baltzer, 1955), Holland (Doeksen, 1948), New Zealand (Nielson, 1951; Sears & Evans, 1953; Waters, 1955), Sweden (Julin, 1937, 1948, 1949; Lindquist, 1938, Sjörs, 1954), Switzerland (Stöckli, 1928, 1949), U.S.A. (Bear, 1929; Eaton & Chandler, 1942; Hopp, 1947; Slater & Hopp, 1947; Smith, 1957), and U.S.S.R. (Dimo, 1938; Baluev, 1950; Ponomareva, 1950, 1953).

Estimates of over 4 and 7 millions per acre have been recorded in Switzerland and Holland (Stöckli, 1949) and of 3 and 5 millions per acre in New Zealand (Waters, 1955). Earthworm numbers vary in relation to soil type and field history (Evans and Guild, 1947) and in old arable land are generally much lower than those quoted above which apply to grassland populations. The biomass of a grassland population of approximately 2 million earthworms per acre has been estimated as about 1000 lb per acre (Reynoldson, 1955).

There are about 28 species of earthworms in the British fauna (Cernosvitov & Evans, 1947; Muldal, 1952; Davies, 1954; Satchell, 1955c), some of which inhabit forest litter, dung, compost heaps and semi-aquatic habitats. About 8-10 species commonly occur in fields, living either at the soil surface, in the topsoil or burrowing into the subsoil.

FEEDING

Present knowledge of earthworm feeding behaviour mainly concerns *Lumbricus terrestris*, a species which draws leaves and other materials into the mouth of its burrow (Müller, 1879, 1884, 1889) besides ingesting soil. It selects, in general, leaves of mull species, such as ash and *Mercurialis*, in preference to those of oak and beech; conifer needles are least acceptable (Darwin, 1881; Henry, 1900; Ramann, 1911; Gast, 1937; Lindquist, 1941; Franz and Leitenberger, 1948; Mangold, 1951; Ponomareva, 1952; Wittich, 1953). Such selection has been ascribed to the shape and texture of the leaves (Darwin, 1881), their mineral content (Gast, 1937), protein content and flavour (Wittich, 1953), while certain leaves which are repellent contain bitter alkaloids or noxious aromatics (Mangold, 1951; Wittich, 1953). Both green and dead leaf fragments have been found in the gut of *L. terrestris*, although Zicsi (1954) considers that the epigeal parts of plants

are only eaten when the worms lack the vitamin A which he considers necessary for the secretion of their saliva. Two other field species, *Allolobophora nocturna* and *A. longa*, have been observed feeding on the surface (Evans, 1947), and the latter has also been found to eat leaves in laboratory tests (Bornebusch, 1953). *Eisenia rosea* and *A. caliginosa*, also common field species, show little inclination to touch leaf litter (Lindquist, 1941), but, like most earthworms, they can be fed in the laboratory on dung, a mature individual of the latter species consuming 20-24 g in a year (Guild, 1955). However, in a fertile, well grazed pasture, root residues have been found to be more important as a food source for *A. caliginosa* than dung or dead herbage (Waters, 1955). There is some evidence that soil micro-organisms may also be a source of food for earthworms. The bacterium, *Serratia marcessens*, was killed out completely in passage through the gut of *L. terrestris* in laboratory cultures (Day, 1950). Aichberger (1914) observed that no diatoms, blue-green algae, desmids, yeasts or rhizopods were found alive in the alimentary canal of earthworms. Müller (1950) thought that *A. caliginosa* probably feeds mainly on fungus mycelium, a speculation to which the subsequent discovery of chitinase in its enzyme system (Tracey, 1951) lends some support. The digestive enzymes of earthworms also include protease, amylase, lipase and cellulase. The enzymes are probably produced by the earthworms themselves, but cellulase and chitinase may possibly also be produced by organisms living in the intestine (Tracey, 1951).

The effect on grassland of earthworm feeding depends to some extent on the rainfall and the drainage of the soil. In low-rainfall areas on chalk soils fissuring, leading to an undesirable loss of water from the subsoil, may start where the sward has been broken by *L. terrestris* feeding on the surface. On wet marginal hill land, on the other hand, reseeding has succeeded better where the breakdown of the old mat before plowing by liming and earthworm activities has resulted in improved drainage (Crompton, 1953).

CASTING

Of the 8-10 common field species only three, *L. terrestris* (Müller, 1879; Bornebusch, 1953), *A. longa* and *A. nocturna*, make casts on the surface of the soil, and at Rothamsted only the two *Allolobophora* species contribute materially to the weight of wormcasts produced (Evans, 1948). Other field species excrete in soil crevices. Casting is generally greater on heavy than on open soils where less soil is eaten during burrowing and more of the faeces are voided in spaces below the surface (Guild, 1955).

Darwin (1881) estimated the annual wormcast production on two old grassland sites as 7.5 and 16.1 tons per acre and similar figures have been obtained at Rothamsted (Evans & Guild, 1947). Estimates from continental Europe range from 2-3 tons per acre in a low-rainfall area of Germany (Kollmannsperger, 1934) to 30-40 tons per acre in Breslau (Dreidax, 1931) and Zürich (Stöckli, 1928). On the assumption that weight for weight the non-casting species of earthworms void the same amount of faeces below the surface as the casting species eject above it, the total soil consumption for all species in eight fields at Rothamsted has been calculated as between 3.7 and 36.3 tons per acre. The time required for the top 4 inches of soil to pass through the alimentary tracts of the earthworm population was estimated as 11½ years for a permanent-pasture field with a high population and 80 years for an arable field with a low population (Evans, 1948). Since these figures are based on a vermifuge sampling method which expels only part of the earthworm population (Evans & Guild, 1947; Reynoldson, 1955; Satchell, 1955b; Svendsen, 1955; Boyd, 1957), it might appear that the soil turnover is more rapid than this, but the estimations are invalid because they assume that all the soil will have passed through the worms before any of it is re-ingested.

EFFECTS ON SOIL STRUCTURE

Earthworm activity is said to affect the physical structure of the soil by comminution of the mineral particles, by increasing the proportion of water-stable aggregates and by the formation of burrows.

Comminution

Evans (1948) found that the amount of coarse sand relative to silt and clay in two old pastures with high earthworm populations increased with depth and suggested that this might be due partly to a reduction of the amount of sand in the upper layers by its comminution in the intestines of earthworms. The presence of a smaller fraction of coarse sand in wormcasts than in soil nearby has been taken as evidence of this process (Teotia *et al*, 1950; Shrikhande & Pathak, 1951; Joshi & Kelkar, 1952), but in some analyses more coarse sand has been found in the casts (Lindquist, 1941; Nijhawan & Kanwar, 1952). The first result could arise if the wormcasts contained more organic matter than the soil or if the worms were selectively ingesting the finer particles; and the second could occur if the casts contained material from a sandier horizon than that from which the soil samples were taken. However, more direct evidence of comminution is available from experiments with earthworms kept in pots in which measurable reductions in size of particles of granite (Bassalik, 1912), basalt (Meyer, 1943) and soil (Blanck & Giesecke, 1924) were obtained. Comminution is thought to increase the base-exchange capacity of soil by exposing new mineral surfaces but how fast this occurs and whether it is of any importance by comparison with normal weathering is unknown.

Soil aggregation

One of the most important effects of earthworm activity is its influence on the crumb structure of fertile mull soils. The main evidence for this is the structure of wormcasts and changes brought about by earthworms in laboratory culture soils. In several studies, wormcasts have been found to contain more water-stable aggregates than non-cast

soil (Bassalik, 1912; Dutt, 1948; Joachim & Panditteseker a, 1948; Swaby, 1949a; Bakhtin & Polsky, 1950; Ponomareva, 1950; Teotia *et al*, 1950; Finck, 1952; Nijhawan & Kanwar, Mamytov, 1953) and in laboratory experiments worm-worked soils have also been found to be more water-stable than unworked soils (Gurianova, 1940; Hopp, 1946; Guild, 1955). The stability of casts from land under grass (Dutt, 1948; Swaby, 1949a; Finck, 1952; Ponomareva, 1953) or lucerne (Gurianova, 1940; Teotia *et al*, 1950; Mamytov, 1953) is much greater than that of casts from land under straw crops, but this difference is also true for uncast soil and may therefore be independent of the earthworms. The stability of casts is said to depend on the availability of nutritive plant residues (Hoeksema *et al*, 1956) and to vary in relation to the feeding behaviour of different species of earthworms (Guild, 1955).

The way in which the aggregates in wormcasts become stabilized is not, however, agreed. One possibility is that the aggregates are simply reinforced mechanically by ingested plant remains such as filaments from vascular bundles (Ponomareva, 1953) and root fragments, but attempts to produce aggregates experimentally from soil and macerated roots were unsuccessful (Swaby, 1949a). A second possibility is that the soil particles are glued together as aggregates by the secretions of the earthworm's intestines (Bakhtin & Polsky, 1950), but this does not account fully for the difference in the stability of casts from grass and arable land. A third possibility is that the stabilizing materials originate from the microflora of the intestine. Wormcasts have been found to contain more water-stable aggregates and more bacteria than soil from their vicinity (Stöckli, 1928; Teotia *et al*, 1950; Kollmannsperger, 1952a; Ponomareva, 1953; Ruschmann, 1953), and casts from grassland contain more water-stable aggregates and more bacteria than casts from arable land (Swaby, 1949a). Since many bacteria produce polysaccharide gums known to be effective aggregators in the laboratory (Peele, 1940; Geoghegan & Brian, 1948) and since organic matter causes soil aggregation only when micro-organisms are present (Waksman & Martin, 1939) it may be that wormcasts are stabilized by polysaccharide gums produced by the earthworm's intestinal bacteria. However there are difficulties in this explanation. Day (1950) could find no consistent differences between the bacterial contents of soil and fresh wormcasts and Dawson (1947) could find no direct relationship between the proportions of water-stable aggregates in casts and soil and the numbers of bacteria present.

Also some bacteria destroy soil aggregates: after casts have been excreted their bacterial population increases (Stöckli, 1928; Dawson, 1947) while their aggregate stability decreases (Hopp & Hopkins, 1946a; Dawson, 1947; Teotia *et al*, 1950). Moreover the amount of polysaccharide gums required to produce good aggregation is probably considerably higher than occurs in the field (Russell, 1950). Aggregation has been obtained experimentally by incubating pasture soil inoculated with a suspension of fresh wormcasts, but this was caused not by bacteria but fungi (Swaby, 1949a) which under field conditions are less numerous in casts than in the original soil (Teotia *et al*, 1950). Earthworms may however influence the formation of aggregates by dispersing fungi in the soil (Hutchinson & Kamel, 1956).

The decrease in the stability of wormcasts after they have been excreted results from the destruction of the soil crumbs by aerobic spore-forming bacteria. During the passage of food through the gut there may be a marked increase in actinomycetes (Ruschmann, 1953, 1954; Schütz & Felber, 1956) which, Ruschmann (1953, 1954) suggests, inhibit aerobic spore-forming bacteria by secreting antibiotics, thus prolonging the stability of the casts. Martin (1945), on the other hand, has shown that actinomycetes may also destroy biologically produced aggregating material.

An alternative explanation of the stability of wormcasts is that the soil particles are cemented by calcium humate synthesised in the worm's intestine from ingested decomposing organic matter and the calcite excreted by the calciferous glands (Meyer, 1943). Calcium humate, when spread as a film over soil particles, is a powerful stabilizing agent (Swaby, 1949b) and may account for the close relationship between the stability of wormcasts and their humus content which has been reported by Ponomareva (1950). However, though a water-stable crumb structure of different soil types shows a direct relationship to humus levels, its formation seems to be due to the cementing effects of filamentous colloids (e.g., pectin) rather than to humic acids and clay minerals. Photomicrographs show the net structure of filamentous colloids in earthworm casts as well as the binding of colloidal quartz particles by mucoid substances excreted by bacterial colonies (Beutelspacher, 1955). Nevertheless casts retain a high stability even after being boiled in acidified H_2O_2 (Nijhawan & Kanwar, 1952), a treatment which would be expected to oxidise not only calcium humate but polysaccharides and the other organic materials which have been postulated as binding agents.

Pore space

The pores between worm-formed aggregates, and the space occupied by earthworm burrows may account for most of the air capacity of some soils. In a garden soil where worms were few and on a golf course with nearly 2 million earthworms per acre burrows were found to occupy respectively 9% and 67% of the soil air space (Stöckli, 1928). Figures of 38% and 66% were obtained by Evans (1948) for a 7-year ley and a pasture in which 10% and 45% respectively of the earthworms were casting species.

In laboratory experiments earthworms have been reported to increase the volume of soil in pot cultures (Wollny, 1890) and to transform a soil of

loose crumbs into a coherent free-draining structure (Frei, 1948). Their activity increased the rate at which water entered barrels of subsoil clay 3-4 times (Hopp & Slater, 1948) and reduced the time taken for water to pass through containers of light sandy loam from 8 to 2 days (Guild, 1955). The effect of earthworm activity on water absorption has also been studied in the field (Read & Walker, 1950) where the deepest burrows, up to 1m (Satchell, 1955b) and 2m (Hoffmeister, 1845; Darwin, 1881; Wilcke, 1953) deep, are made by *L. terrestris*. In seven sites where the earthworm populations were high, the average infiltration rate was 8 times that of seven comparable sites with low populations (Slater & Hopp, 1947).

These observations suggest that where earthworm populations are high they materially affect soil aeration, drainage and water absorption and, under certain circumstances, limit soil erosion by reducing run-off (Hopp, 1946).

Worm-worked soils have also been found to contain a higher proportion of capillary to non-capillary water than unworked soils. The light sandy loam studied by Guild (1955) became waterlogged at 25% water content in the absence of earthworms, but, when worked by *A. longa*, it held the same amount of water in the capillaries within the soil aggregates, allowing continuous gaseous diffusion between them. The effect of the earthworms in increasing the amount of water which the soil could hold without becoming waterlogged was related to an increased colloid content derived from the dung which the worms had eaten. The conversion of organic residues by earthworms to colloids with a high water-retaining capacity may account also for the reduced loss of moisture by evaporation in worm worked soils noted by Russell (1910) and Zicsi (1954). Archangelskii (1929) found that the activity of earthworms increased the proportions of capillary to non-capillary pore space, but states that they slightly reduced the soils' 'humidity capacity'.

EFFECTS ON SOIL CHEMISTRY

Wormcasts and soil from the same neighbourhood have been compared chemically by several workers (Dusserre, 1902; Powers & Bollen, 1935; Lunt & Jacobson, 1944; Stöckli, 1949; Ponomareva, 1950; Finck, 1952; Nye, 1955). Their results show that casts generally have a higher base-exchange capacity and are richer in some or all of the following: total and exchangeable calcium; exchangeable potassium and manganese; available phosphorus; total exchangeable bases and total organic matter. Since the increase of these materials is derived from the plant remains which the worms ingest, the claim that earthworms increase the supply of plant nutrients cannot be maintained on the basis of comparisons of their faeces with soil samples. Nye (1955) found that the proportions of exchangeable cations in casts in Nigeria agreed well with the relative amounts in the leaves overlying them, and in pot experiments where the whole of the soil and not the casts alone was sampled no chemical difference was found between soils which had contained worms for four months and soils without worms (Frei, 1948). Earthworm activity may nevertheless have far-reaching chemical consequences arising from its effect on soil structure. Bloomfield (1955) has shown that the difference between podzolizing and non-podzolizing species of tree may be determined partly by the extent to which sesquioxides mobilized by leaf leachates are resorbed by soil colloids. Earthworms, described by Powers & Bollen (1935) as colloid mills, may to some extent counteract the process of podzolization by producing colloidal material from the soil and organic matter passing through their intestines.

Soil Reaction

The misconception that earthworms feed at random on the soil has sometimes led to the conclusion that, since their casts are usually more nearly neutral than soil from their vicinity (Salisbury, 1923; Stöckli, 1928, 1949; Dotterweich, 1933; Finck, 1952; Nye, 1955) or than unworked soil in pot cultures (Puh, 1941), earthworms tend to neutralize soil reaction. This action was formally attributed to calcite crystals which are excreted by the calciferous glands of earthworms when calcium in excess of their requirements is present in either the soil (Robertson, 1936; Baltzer, 1955) or ingested plant materials (Puh, 1941; Ponomareva, 1948). Calcite crystals do not dissociate at the pH prevailing in the gut and it is now realized that they have no reaction on the gut contents and that the cause of the neutralization is the secretions of the intestine as a whole (Robertson, 1936). Ammonia, which forms a large proportion of the nitrogenous matter excreted by earthworms (Cohen & Lewis, 1949) may cause a temporary rise in soil pH. The importance of the effect of earthworms on the reaction of agricultural soils has not been assessed.

Soil Nitrogen

Since earthworms increase both soil aeration and bacterial populations (Heymons, 1923; Anstett, 1951), it is possible they favour nitrification (Keller, 1893; Ribaucourt & Combault, 1907; Keup, 1913; Blanck & Giesecke, 1924; Stöckli, 1928; Archangelskii, 1929; Lang, 1931; Puh, 1941). There is no evidence that nitrogen-fixing bacteria increase during passage through the earthworm intestine (Day, 1950; Khambata & Bhat, 1957), indeed *Azotobacter* has been found to decrease there (Ruschmann, 1953; 1954) but may increase considerably outside the gut in cast soil (Stöckli, 1928). Several workers have recorded an increase in nitrate nitrogen in soils in which earthworms were reared (Russell, 1910; Blanck & Giesecke, 1924; Archangelskii, 1929; Lindquist, 1941; Hopp & Slater, 1949a), but in most of these experiments some of the worms died and the increase could be accounted for by the nitrification of their bodies. The protein content of earthworm tissue is high, (Kollmannsperger, 1952b; Watson & Smith, 1956), 54-72% of the dry weight (Lawrence & Miller, 1945; French *et al*, 1957) and may yield on decomposition an average of 10 mg of nitrate

nitrogen per worm (Russell, 1910). From this figure, Russell (1910) calculated that a population of 25,000 earthworms per acre, an estimate for arable land attributed to Hensen (1877), could yield the nitrate-nitrogen equivalent of only 3¼ lb of nitrate of soda per acre. This figure is, however, quite invalid since Hensen referred only to the numbers of *L. terrestris* and not to the whole earthworm population. If the calculation is based instead on a population of 1½ millions per acre, a moderate figure for grassland, the possible nitrate yield reaches the equivalent of 195 lb of nitrate of soda per acre. The actual rate of mineralization of this considerable nitrogen reserve cannot at present be calculated since insufficient is known of the mortality rates of earthworms under field conditions. In the laboratory, individual specimens of *A. longa* have lived for as long as 10¼ years (Korschelt, 1914), but other species, e.g., *L. castaneus*, appear to have an average adult life of only a few months (Evans & Guild, 1948a). However, Hopp (1947) found that the earthworm biomass of grassland in the U.S. fell by about three-quarters during the summer months so that the annual return of nitrogen from this source may be sufficient to have a considerable influence on the yield of vegetation.

In forest soils the proportion of N as α-amino acids has been found (Wittich, 1952) to increase with improving quality of humus, and there is evidence of an increased α-amino-N production in the presence of great earthworm activity.

Needham (1957) has recently reported that no measurable quantities of nitrogen were detected in the solid faecal matter of earthworms fed on elm leaves which contained 6.6 mg of nitrogen per gram dry weight. This suggests that earthworms are exceptionally efficient in metabolizing the nitrogen of plant material, but the question remains whether the nitrogen reaching the vegetation through the channel of earthworm excretion and the mineralization of their tissues would be as efficiently mobilized in other ways if the earthworms were absent. Richardson (1938) found that grass litter, which broke down rapidly when mixed with soil, remained as a thick surface mat on acid plots where worms were absent, although on the more normal soil used by Russell (1910) in his pot experiments, organic matter seemed to decompose equally quickly whether worms were present or not. In pot experiments, Archangelskii (1929) found that nitrogen deficiency caused by incorporating straw and manure in the soil reduced the yield of barley and oats, but the presence of earthworms in the pots decreased this effect. The importance of earthworms relative to other channels of nitrogen mobilization requires further study.

EFFECTS ON CROP YIELD

It might seem a straightforward matter, if the claims made for earthworms are justified, to demonstrate their beneficial effects in increased crop yields. These have indeed been obtained in numerous experiments (Wollny, 1890, 1897; Russell, 1910; Kahsnitz, 1922; Archangelskii, 1929; Powers & Bollen, 1935; Puh, 1941; Hopp & Slater, 1948, 1949a; Baluev, 1950; Joshi & Kelkar, 1952; Uhlen, 1953; Spannagel, 1954) where earthworms were kept in containers and either fertilized the soil with their dead bodies (Russell, 1910; Hopp & Slater, 1949a; Uhlen, 1953) or improved its aeration or drainage (Kahsnitz, 1922; Archangelskii, 1929; Hopp & Slater, 1948). In a similar experiment earthworms decreased the yield of mixed clover and grasses (Stebler *et al* 1904), although they increased the percentage of clover in the mixture. Evans (in Russell, 1950), using spinach as a test crop, obtained an increase in dry weight but not of fresh weight, a result which might have been caused by improved soil structure. However, the conditions of plant growth may be very different in the field from those in pot experiments and the results of these experiments are inconclusive.

Chadwick and Bradley (1948) experimented on a larger scale with both outdoor and greenhouse plots. Earthworms of two sorts were used, *A. caliginosa*, a field species, and worms sold commercially as hybrids which were in fact mainly *Eisenia foetida*, a species which requires the conditions of manure or compost heaps for survival (Wilcke, 1952). The latter species died except where dung was liberally applied and their addition to the plots had little effect on the yield perhaps because the numbers used in the main experiment with this species were small, equivalent to less than 60,000 per acre. The experiment with *A. caliginosa* also employed rather few worms, the equivalent of about 400,000 per acre, but the plots containing them yielded higher average dry weights of zinnia plants and dahlia roots than control plots, possibly due to a manurial effect from dead earthworms. Plots with and without *A. caliginosa* yielded the same dry weights of phlox and chrysanthemum plants. The worms appeared to have no effect on soil aggregation but as the experiment was run from March to September and *A. caliginosa* is generally aestivating during most of this period this is not surprising. The experiments with *E. foetida* refute the claims of the commercial suppliers, but the investigations are otherwise rather inconclusive.

Uhlen (1953), using barley as a test crop in outdoor frames, found that in heavily manured soils the greatest yields were obtained in soil containing large numbers of live *L. terrestris* and *L. rubellus*; these species probably contributed more than others to the decomposition of the manure. In unfertilized soils however the greatest yields were obtained in the soils in which most of the worms had died. Frames stocked with mixed populations of earthworms in numbers equal to high field populations yielded 5% more barley than unstocked frames.

An increase of 7.4% in yield of winter wheat was similarly obtained by Dreidax (1931) from plots into which 84 g/sq m of living worms had been introduced. On plots to which 54 g/sq m of dead worms had been added the yield was 15.3% higher

than that of plots to which no worms had been added. The N content of the crop from the plots into which live worms had been introduced was 21% higher than that from control plots and about equal to that from plots treated with dead worms. About half of the 21% increase was ascribed to the effects of worm activity and half to the manurial effects of worms which had died during the experiment. The increased crop yield obtained by Ribaucourt & Combault (1907) from a field to which living earthworms had been added may similarly have been due largely to the fertilizing effect of worms which had died during the experiment.

Van der Drift (1955) also found that earthworms (*L. rubellus*) introduced to experimental plots failed to survive except where the plots had been marled. The absence of earthworms from soil is generally an indication that conditions are unsuitable for them, but where they are absent for zoogeographical reasons it may be possible to establish populations artificially without first altering the soil conditions (Hamblyn & Dingwall, 1945; Nielson, 1951). In such an area in New Zealand, Nielson (1953) recorded an increase in the proportion of clover in grassland a few years after it had been invaded by earthworms. These observations and similar results obtained experimentally (Stebler *et al*, 1904; Hopp & Slater, 1948) suggest that earthworms favour the growth of clover, but two other workers who found a relationship between earthworm numbers and the abundance of clover in the field regarded it as due to the influence on both clover and earthworms of grazing (Bates, 1933) or soil reaction (Satchell, 1955a). The difficulties of establishing earthworm populations artificially without first changing the soil conditions it is desired to study and without obscuring the effects of earthworm activity with manurial effects arising from high mortality, are formidable. An alternative approach at present being investigated (Dobson & Lofty, 1956) is to destroy the naturally existing population of earthworms in selected areas and to observe any deterioration in the soil and crop yield which may ensue.

EFFECTS OF CULTIVATION, FERTILIZERS, AND TOXIC CHEMICALS ON EARTHWORM POPULATIONS

Cultivation

When grassland is plowed the earthworm population may be reduced by 70% within 5 years of cultivation (Evans & Guild, 1948b). Three factors appear to contribute to this: mechanical damage, loss of the insulating herb layer and reduced food supplies. Rotary cultivation may cause serious damage to the earthworms in the topsoil, but normal plowing has little effect (Krüger, 1952; Tischler, 1955), the population remaining unchanged by the first plowing-in of the sward (Evans & Guild, 1948b). Investigations of cropland in the U.S.A. show that the main fall in numbers, which can be prevented by leaving the crop residues on the soil, occurs there during autumn frosts (Hopp & Hopkins, 1946b; Hopp & Linder, 1947; Slater & Hopp, 1947; Hopp & Slater, 1949b; Teotia *et al*, 1950), but this factor is probably less important in the milder winters of the U.K. Food supplies are commonly the principle factor limiting earthworm populations in both grassland (Waters, 1955; Hoeksema *et al*, 1956; Jefferson, 1956) and arable land, and the reduction of earthworm numbers by cultivation has been attributed primarily to the decrease of suitable plant residues (Evans & Guild, 1948b). Stubble-mulching has been found to increase earthworm populations (McCalla, 1953) and where food is supplied by heavy manuring, arable land can maintain populations exceeding one million per acre (Morris, 1922; Evans, 1947; Tischler, 1955); in the U.S. where arable land was protected by crop residues from frost the population level exceeded that of adjacent grassland (Slater & Hopp, 1947). In Britain the advantages of autumn plowing almost certainly outweigh those of protecting the earthworm population from frost; and heavy organic manuring is hardly likely to be extended at present. Increased insulation from frost and suitable food materials are however provided by leys, especially if they contain legumes, since these are rich in protein (Johnstone-Wallace, 1937) and appear to be particularly palatable to earthworms (Hopp, 1946; Forster, 1950; Teotia *et al*, 1950; Ponomareva, 1952; Mamytov, 1953; Sears & Evans, 1953; Watkin, 1954). Evans & Guild (1948) found that two-year-old leys previously cultivated for two years contained as many earthworms of all species except *A. nocturna* as the original permanent pasture, but recovery may be delayed if the soil becomes too compacted by heavy stocking (Low, 1955). Ley farming seems to be the most practical form of earthworm conservation.

Fertilizers

The effect of inorganic fertilizers on earthworm populations depends on whether they increase or decrease soil acidity. Thus lime, nitro-chalk, nitrate of soda and basic slag tend to increase earthworm populations, and sulphate of ammonia, sulphate of potash and super-phosphate have the opposite tendency (Escritt & Arthur, 1948). Reduction of earthworm populations from this cause is, however, negligible unless the soil reaction falls below pH 4.5-5.0 (Jefferson, 1955; Satchell, 1955a) and this does not occur when normal amounts of fertilizers and lime are applied (Ogg & Nicol, 1945). The effect of lime in increasing earthworm populations (Crompton, 1953) has been ascribed to its influence in decomposing organic matter to a condition suitable for earthworms to eat it (Escritt & Arthur, 1948; Jefferson, 1956), but non-nutritional responses may also be involved. In pot, frame and field tests, Uhlen (1953) could find no effect of commercial fertilizers on earthworms, but Johnstone-Wallace (1937) found that application of superphosphate and lime to a pasture produced a dense sward of wild white clover and increased the weight of earthworms about fourfold. On arable land receiving dressings of mineral fertilizers, Evans (in Ogg &

Nicol, 1945) and Jakob & Wiegand (1952) similarly found more worms than on unfertilized plots, the result probably of increased root residues. Heavy applications of nitro-chalk to sheep-grazed pasture have also been found to increase earthworm populations indirectly by stimulating grass production and hence increasing the amount of dung returned to the soil (Watkin, 1954).

Insecticides and Herbicides

The effects of soil treatment with BHC, DDT and parathion on soil fauna have recently been reviewed (Satchell, 1955d). Hoy (1955) found that dressings of crude BHC dust at the rate of 21 lb/acre of the gamma isomer killed all the earthworms in pots of soil of low organic-matter content, but a similar dressing had no effect on earthworms in soil of moderate organic-matter content. Other workers (Gunthart, 1947; Prisyazhnyuk, 1950; Grigoreva, 1952; Richter, 1953; Weber, 1953) found no increase in earthworm mortality after applying BHC dust even at a rate of 500 kg/ha. Two authors (Gunthart, 1947; Goffart, 1949) have, however, reported high earthworm mortality following the application of liquid formulations of BHC.

The situation is similar with DDT. Emulsions (Baker, 1946; Gunthart, 1947) and heavy applications of dust (Greenwood, 1945; Polivka, 1951; Hoy, 1955) killed earthworms in pot experiments or reduced field populations, but dressings containing up to 40 lb/acre of the effective isomer appear to be harmless (Goffart, 1949; Fleming & Hawley, 1950; Hoy, 1955). Parathion is more toxic to earthworms than either BHC or DDT (Weber, 1953) and its effects have been found to persist for at least two months (Goffart, 1949).

The herbicides 2M4K and 2-4D have been found to have no effect on earthworm populations (Uhlen, 1953; Weber, 1953).

In general, pest and weed-control chemicals, with the exception of parathion, have not been found to reduce earthworm numbers seriously when used at normal rates of application.

Radio-active isotopes

It is recognized that there is now extensive pollution of the soil by radio-active fall-out, and it has been postulated that dispersal of the radio-active substances is accelerated by the capacity of living organisms to accumulate the isotopes within their tissues (Peredel'sky, 1957). Peredel'sky, *et al* (1957) recently found that plants growing 20 cm away from a source of ^{60}Co in the soil accumulated more of the isotope in soil containing earthworms than in soil without earthworms and concluded that earthworms will dissipate accumulations of isotopes in the soil and bring the level to more natural proportions. It was also found that *Brassica* sp grown on contaminated soil accumulated more than five times the amount of ^{60}Co when earthworms were present than when they were absent. As only a small proportion of the earthworms introduced were recovered after the experiment, the increase of ^{60}Co taken up by the plants was probably from the decomposed tissues of earthworms which had died.

CONCLUSIONS

It has been demonstrated that earthworm activity can accelerate the decay of plant remains, aggregate soil particles, improve drainage and aeration, and conserve soil moisture. For the most part these demonstrations have been only qualitative or on a small scale and, though valuable as pilot experiments, provide no basis for estimating the importance of earthworms under field conditions. This applies particularly to laboratory demonstrations of improved crop yields in the presence of worms and at present the evidence on the desirability of earthworm-conservation measures is insufficient to justify changes in normal agricultural practice. Ecological studies have reached the stage where physiological research into earthworm metabolism, particularly nutrition, excretion and sense physiology is needed. An integration of future ecological and physiological research is essential for an understanding of the relationship between earthworms and soil fertility.

References

AICHBERGER, R. VON. 1914. [Studies on the nutrition of earthworms.] *Kleinwelt* **6**, 53-58, 69-72, 85-88. [G.]

ANSTETT, A. 1951. [On the macrobiological activation of humification processes.] *C.R. Agric. Fr.* **37**, 262-264. [F.]

ARCHANGEL'SKII, M. P. 1929. [On the influence of the activity of earthworms on the yield of oats and barley in relation to fertilizer addition.] *J. landw. Wissensch. Moskau* **6**, 849-862. [R.e.]

BAKER, W. L. 1946. DDT and earthworm populations. *J. econ. Ent.* **39**, 404-405.

BAKHTIN, P. U. and POLSKY, M. N. 1950. [The role of earthworms in structure formations of sod-podzolized soils.] *Pochvovedenie* 487-491. [R.]

BALTZER, R. 1955. [Earthworm fauna and soil type.] *Z. PflErnahr. Dung.* **71**, 246-252. [G.]

BALUEV, V. K. 1950. [Earthworms of the basic soil types of the Ivanov region.] *Pochvovedenie* 219-227. [R.]

BASSALIK, K. 1913. [On silicate decomposition by soil bacteria.] *Z. Gärungsphyiol.* **2**, 1-32. [G.]

BATES, G. H. 1933. The distribution of wild white clover (*Trifolium repens*) in relation to the activity of earthworms (Lumbricidae). *Welsh J. Agric.* **9**, 195-208.

BEAR, F. E. 1929. Fertilizers. Pp. 360. *Wiley, New York.*

BEUTELSPACHER, H. 1955. [Natural filamentous colloids and crumb formation.] *Landb.-Forsch.* **5**, 90-92. [G.]

BLANCK, E. and GIESECKE, F. 1924. [The effect of earthworms on the physical and biological properties of soil.] *Z. Pflanz. Düng.* **3**(B), 198-210. [G.]

BLOOMFIELD, C. 1955. A study of podzolization. VI. The immobilization of iron and aluminium. *J. Soil Sci.* **6**, 284-292.

BORNEBUSCH, C. H. 1930. The fauna of the forest soil. *Forstl. Forsøksv. Danm.* **11**, 1-224.

BORNEBUSCH, C. H. (Edited by Hølstener-Jorgensen, H.). 1953. [Laboratory experiments on the biology of earthworms.] *Dansk Skovforen. Tidsskr.* **38**, 557-579. [Da.]

BRETSCHER, K. 1896. [The Oligochaeta of Zürich.] *Rev. Suisse Zool.* **3**, 499-532. [G.]

BOYD, J. M. 1957. The Lumbricidae of a dune-*machair* soil gradient in Tiree Argyll. *Ann. Mag. nat. Hist.* Ser. 12, **10,** 274-282.

CERNOSVITOV, L. and EVANS, A. C. 1947. The Linnean Society of London. Synopses of the British Fauna. No. 6. Lumbricidae. London.

CHADWICK, L. C. and BRADLEY, K. 1948. An experimental study of the effects of certain earthworms on crop production. *Proc. amer. Soc. hort. Sci.* **51,** 552-562.

COHEN, S. and LEWIS, H. B. 1949. Nitrogenous metabolism of the earthworm (*Lumbricus terrestris*). *Fed. Proc.* **8,** 191.

CROMPTON, E. 1953. Grow the soil to grow the grass. Some pedological aspects of marginal land improvement. *J. Minist. Agric.* **50**(7), 301-308.

DARWIN, C. 1837. On the formation of vegetable mould. *Trans. geol. Soc. Lond. 2nd Ser.*, **5**(3), 505-509. (1840).

DARWIN, C. 1881. The Formation of Vegetable Mould through the Action of Worms, with Observations on their Habits. *Murray, London.*

DAVIES, H. 1954. On the occurrence in England of the earthworm *Allolobophora arnoldi* Gates, 1952. *Ann. Mag. nat. Hist.* Ser. 12, **8,** 351-2.

DAWSON, R. C. 1947. Earthworm microbiology and the formation of water-stable aggregates. *Soil Sci. Soc. Amer. Proc.* **12,** 512-516.

DAY, G. M. 1950. The influence of earthworms on soil microorganisms. *Soil Sci.* **69,** 175-184.

DIMO, N. A. 1938. [Earthworms in the soils of Middle Asia.] *Pochvovedenie* No. 4, 494-526. [R.e.]

DOBSON, R. M. and LOFTY, J. R. 1956. Rehabilitation of marginal grassland. *Rep. Rothamst. exp. Stat. 1956,* 154-155.

DOEKSEN, J. 1948. [Earthworms.] *Maandbl. Landb. VoorlDienst* **5,** 113-117. [Du.]

DOEKSEN, J. 1950. An electrical method of sampling soil for earthworms. *Trans. 4th int. Congr. Soil Sci.*, 129-131.

DOTTERWEICH, H. 1933. [The function of storage of calcium by animals as a buffer reserve in the regulation of reaction. The calciferous glands of earthworms.] *Pflüg. Arch. ges. Physiol.* **232,** 263-286. [G.]

DREIDAX, L. 1931. [Investigations on the importance of earthworms for plant growth.] *Arch. Pflanzenbau* **7,** 413-467.

DRIFT, J. VAN DER. 1950. Analysis of the animal community in a beech forest floor. *Tijdschr. Ent.* **94,** 1-168.

DRIFT, J. VAN DER. 1955. [Influence of earthworms on humus formation.] *Tuinbouwk. Onderz. Jversl. 1954,* 31-32. [Du.]

DUSSERRE, C. 1902. [On the effect of earthworms on the chemical condition of soils.] *Landw. Jb. Schweiz* **16,** 75-78. [G.]

DUTT, A. K. 1948. Earthworms and soil aggregation. *J. amer. Soc. Agron.* **40,** 407-410.

EATON, T. H. JR. and CHANDLER, R. F. JR. 1942. The fauna of forest-humus layers in New York. *Cornell agric. Exp. Stat. Mem.* **247,** 1-26.

EDWARDS, E. E. 1929. A survey of the insect and other invertebrate fauna of permanent pasture and arable land of certain soil types at Aberystwyth. *Ann. appl. Biol.* **16,** 299-323.

ESCRITT, J. R. and ARTHUR, J. H. 1948. Earthworm control—a resumé of methods available. *J. Bd Greenkeep. Res.* **7**(24), 162-172.

EVANS, A. C. 1947. Earthworms. *J. Bd Greenkeep. Res.* **7**(23), 49-54.

EVANS, A. C. 1948. Studies on the relationships between earthworms and soil fertility. II. Some effects of earthworms on soil structure. *Ann. appl. Biol.* **35**(1), 1-13.

EVANS, A. C. and GUILD, W. J. MCL. 1947. Studies on the relationships between earthworms and soil fertility. I. Biological studies in the field. *Ann. appl. Biol.* **34**(3), 307-330.

EVANS, A. C. and GUILD, W. J. MCL. 1948(a). Studies on the relationships between earthworms and soil fertility. IV. On the life cycles of some British Lumbricidae. *Ann. appl. Biol.* **35**(4), 471-484.

EVANS, A. C. and GUILD, W. J. MCL. 1948(b). Studies on the relationships between earthworms and soil fertility. V. Field populations. *Ann. appl. Biol.* **35**(4), 485-493.

FINCK, A. 1952. [Ecological and pedological studies on the effects of earthworms on soil fertility.] *Z. PflErnähr. Düng.* **58**(103), 120-145. [G.]

FLEMING, W. E. and HAWLEY, I. M. 1950. A large-scale test with DDT to control the Japanese Beetle. *J. econ. Ent.* **39,** 677-678.

FORD, J. 1935. The animal population of a meadow near Oxford. *J. Anim. Ecol.* **4**(2), 195-207.

FORSTER, H. C. 1950. Soil fertility and the interaction of plant with animal. *J. aust. Inst. agric. Sci.* **16,** 44-52.

FRANZ, H. 1950. [Soil Zoology as a Basis for Soil Management.] *Berlin (Akademie Verlag).* [G.]

FRANZ, H. and LEITENBERGER, L. 1948. [Biological-chemical investigations into the formation of humus through soil animals.] *Ost. zool. Z.* **1**(5), 498-518. [G.]

FREI, E. 1948. [Studies of soil fabric in agricultural soils.] *Landw. Jb. Schweiz* **62,** 20-36. [G.f.]

FRENCH, C. E., LISCINSKY, S. A. and MILLER, D. R. 1957. Nutrient composition of earthworms. *J. Wildlife Mgmt* **21**(3), 348.

GALOUX, A. 1953. [The sessile oakwood of the Haute Campine.] *Trav. Sta. Rech. Groenendael,* Ser. A., No. 8, 1-235. [F.]

GAST, P. R. 1937. Contrast between the soil profiles developed under pines and hardwood. *J. For.* **35,** 11-16.

GEOGHEGAN, M. J. and BRIAN, R. C. 1948. Aggregate formation in soil. I. Influence of some bacterial polysaccharides on the binding of soil particles. *Biochem. J.* **43,** 5-13.

GOFFART, H. 1949. [The action of new insecticides on earthworms.] *Anz. Schädlingsk.* **22,** 72-74. [G.]

GRAFF, O. 1953. [Investigations in soil zoology with special reference to the terricole Oligochaeta.] *Z. PflErnähr. Düng.* **61,** 72-77. [G.]

GREENWOOD, D. E. 1945. Wireworm investigations. *Conn. agric. Exp. Sta. Bull.* **488,** 344-347.

GRIGOR'EVA, T. G. 1952. [The effect on the soil fauna of hexachlorane applied to the soil.] *Dokl. Akad. s.-kh. Nauk* No. 12, 16-20. [R.]

GUILD, W. J. MCL. 1948. Studies on the relationship between earthworms and soil fertility. III. The effect of soil type on the structure of earthworm populations. *Ann. appl. Biol.* **35**(2), 181-192.

GUILD, W. J. MCL. 1951. The distribution and population density of earthworms (Lumbricidae) in Scottish pasture fields. *J. Anim. Ecol.* **20**(1), 88-97.

GUILD, W. J. MCL. 1952a. The Lumbricidae in upland areas. II. Population variation on hill pasture. *Ann. Mag. nat. Hist.* Ser. 12, **5,** 286-292.

GUILD, W. J. MCL. 1952b. Variation in earthworm numbers within field populations. *J. Anim. Ecol.* **21,** 169-181.

GUILD, W. J. MCL. 1955. Earthworms and soil structure. *Soil Zoology (Proc. Nottingham Sch. agric. Sci.),* 83-98.

GUNTHART, E. 1947. [The control of cockchafer larvae with Hexachlorcyclohexane preparation.] *Mitt. schweiz. ent. Ges.* **20,** 409-450. [G.]

GURIANOVA, O. Z. 1940. [The influence of earthworms on the development of structure in chernozem soils.] *Pochvovedenie* No. 4, 99-107. [R.]

HAMBLYN, C. J. and DINGWALL, A. R. 1945. Earthworms. *N.Z. J. Agric.* **71,** 55-58.

HENRY, E. 1900. [Feeding experiments on earthworms with beech, oak and hornbeam leaves.] *J. Agric. prat.,* 778. [F.]

HENSEN, V. 1877. [The role of earthworms (*Lumbricus terrestris* L.) in soil fertility.] *Z. wiss. Zool.* **28,** 354-364. [G.]

HEYMONS, R. 1923. [The influence of earthworms on the structure and yield of soils.] *Z. Pflanz. Düng.* **2**(A), 97-129. [G.]

HOEKSEMA, K. J., JONGERIUS, A. and MEER, K. VAN DER. 1956. [On the influence of earthworms on the soil structure in mulched orchards.] *Boor en Spade* **8,** 183-201. [Du.e.]

HOFFMEISTER, W. 1845. [The known Species of Earthworms.] *Braunschweig.* Pp. 43. [G.]

HOPP, H. 1946. Earthworms fight erosion too. *Soil Conserv.* **11,** 252-254.

HOPP, H. 1947. The ecology of earthworms in cropland. *Soil Sci. Soc. Amer. Proc.* **12,** 503-507.

HOPP, H. and HOPKINS, H. T. 1946a. Earthworms as a factor in the formation of water-stable soil aggregates. *J. Soil Wat. Conserv.* **1**(1), 11-13.

HOPP, H. and HOPKINS, H. T. 1946b. The effect of cropping systems on the winter population of earthworms. *J. Soil Wat. Conserv.* **1**(1), 85-88, 98.

HOPP, H. and LINDER, P. J. 1947. A principle for maintaining earthworms in farm soils. *Science* **105,** 663-664.

HOPP, H. and SLATER, C. S. 1948. Influence of earthworms on soil productivity. *Soil Sci.* **66,** 421-428.

HOPP, H. and SLATER, C. S. 1949a. The effect of earthworms on the productivity of agricultural soil. *J. agric. Res.* **78,** 325-339.

HOPP, H. and SLATER, C. S. 1949b. A principle for maintaining structure in clean-cultivated soils. *J. agric. Res.* **78,** 347-352.

HOY, J. M. 1955. Toxicity of some hydrocarbon insecticides to earthworms. *N.Z. J. Sci. Tech., Sect. A.* **37**(4), 367-372.

HUTCHINSON, S. A. and KAMEL, M. 1956. The effect of earthworms on the dispersal of soil fungi. *J. Soil Sci.* **7**(2), 213-218.

JACOB, A. and WIEGLAND, K. 1952. [Transformations of the mineral nitrogen of fertilisers in the soil.] *Z. PflErnähr. Düng.* **59,** 48-60. [G.]

JEFFERSON, P. 1955. Studies on the earthworms of turf. A. The earthworms of experimental turf plots. *J. Sports Turf Res. Inst.* **9**(31), 6-27.

JEFFERSON, P. 1956. Studies on the earthworms of turf. B. Earthworms and soil. *J. Sports Turf Res. Inst.* **9**(32), 166-179.

JOACHIM, A. W. R. and PANDITTESEKERA, D. G. 1948. Soil fertility studies. IV. Investigations on crumb structure and stability of Cocal soils. *Trop. Agriculturist* **104,** 119-129.

JOHNSTONE-WALLACE, D. B. 1937. The influence of wild white clover on the seasonal production and chemical composition of pasture herbage and upon soil temperatures, soil moisture and erosion control. *4th int. Grassl. Congr. Rep.*, 188-196.

JOSHI, N. V. and KELKAR, B. V. 1952. The role of earthworms in soil fertility. *Indian J. agric. Sci.* **22,** 189-196.

JULIN, E. 1937. [Ågård, a deciduous forest region of S.W. Småland.] *Sveriges Natur* **28**. [Sw.]

JULIN, E. 1948. [Vessers Udde. Soil and vegetation in a park meadow reverting to woodland.] *Acta phytogeogr. Suec.* **23,** 1-186. [Sw.g.]

JULIN, E. 1949. [The Swedish earthworms.] *Ark. Zool.* **42**(A), 1-58. [Sw.e.]

KAHSNITZ, H. G. 1922. [Investigations on the influence of earthworms on soil and plant.] *Bot. Arch.* **1,** 315-331. [G.]

KELLER, C. 1893. [The Animal World in Agriculture.] *Leipzig*. [G.]

KEUP, E. 1913. [Feeding and activity of earthworms in relation to agriculture.] *Mitt. deutsch. landw. Ges.* **28,** 538-542. [G.]

KHAMBATA, S. R. and BHAT, J. V. 1957. A contribution to the study of the intestinal microflora of Indian earthworms. *Arch. Mikrobiol.* **28,** 69-80.

KOLLMANNSPERGER, F. 1934. [The Oligochaeta of the Bellinchen Region.] *Inaugural Dissertation. Dillingen (Saargebiet)*. [G.]

KOLLMANNSPERGER, F. 1952a. [The importance of earthworms for soil fertility.] *Decheniana* **105/106,** 165-187.

KOLLMANNSPERGER, F. 1952b. [Can earthworms be utilised and are they poisonous?] *Decheniana* **105/106,** 189-193. [G.]

KORSCHELT, E. 1914. [On transplantation experiments, diapause and longevity of Lumbricidae.] *Zool. Anz.* **43,** 537-555. [G.]

KRÜGER, W. 1952. [Influence of cultivation on the fauna of fields (A study in agricultural ecology.] *Z. Acker- u. Pflbau* **95,** 261-302. [G.]

LANG, R. 1931. [Real and apparent crumb structure and tilth.] *Forstwiss. Cbl.* **53,** 309-324, 351-367, 393-403. [G.]

LAWRENCE, R. D. and MILLER, H. R. 1945. Protein content of earthworms. *Nature Lond.* **155,** 517.

LINDQUIST, B. 1938. Dalby Söderskog. *Acta phytogeogr. Suec.* Part X, 1-273. [Sw.]

LINDQUIST, B. 1941. [Investigations on the significance of some Scandinavian earthworms in decomposition of leaf litter and the structure of mull soil.] *Svenska SkogsvFören. Tidskr.* **39**(3), 179-242. [Sw.g.]

LOW, A. J. 1955. Improvements in the structural state of soils under leys. *J. Soil Sci.* **6,** 179-199.

LUNT, H. A. and JACOBSON, G. M. 1944. The chemical composition of earthworm casts. *Soil Sci.* **58,** 367-375.

MAMYTOV, A. 1953. [The effect of earthworms on the water stability of mountain-valley serozem soils.] *Pochvovedenie* No. 8, 58-60. [R.]

MANGOLD, O. 1951. [Experiments in analysis of the chemical senses of earthworms. I. Methods and procedure for leaves of plants.] *Zool. Jb. (Physiol.)* **62,** 441-512. [G.]

MARTIN, J. P. 1945. Microorganisms and soil aggregation. I. Origin and nature of some of the aggregating substances. *Soil Sci.* **59,** 163-174.

MCCALLA, T. M. 1953. Microbiological studies of stubble mulching. *Neb. agric. Exp. Sta. Bull.* **417,** 1-14.

MEYER, L. 1943. [Experimental study of macrobiological effects on humus and soil formation.] *Bodenk. u. PflErnähr.* **29**(74), 119-140. [G.]

MORRIS, H. M. 1922. Insect and other invertebrate fauna of arable land at Rothamsted. *Ann. appl. Biol.* **9**(3/4), 282-305.

MULDAL, S. 1952. A new species of earthworm of the genus *Allolobophora*. *Proc. zool. Soc. Lond.* **122,** 463-465.

MÜLLER, P. E. 1879. [Forest-soil studies, a contribution to silvicultural theory. I. Concerning beech mull and beech mor on sands and clays.] *Tidsskr. Skogbruk* **3,** 1-124. [Da.]

MÜLLER, P. E. 1884. [Forest-soil studies, a contribution to silvicultural theory. II. On mull and mor in oak forests and on heaths.] *Tidsskr. Skogbruk* **7,** 1-232. [Da.]

MÜLLER, P. E. 1889. [Researches on the natural forms of humus and their influence on vegetation and the soil.] *Ann. Sci. agron. Nancy* **6,** 85-423. [F.]

MÜLLER, P. E. 1950. [Forest-soil studies, a contribution to silvicultural theory. III. On compacted ground, deficient in mull, especially in beech forests.] *Dansk. Skovför. Tidsskr.* **1,** 10-61. [Da.]

NEEDHAM, A. E. 1957. Components of nitrogenous excreta in the earthworms *Lumbricus terrestris*, L. and *Eisenia foetida* (Savigny). *J. exp. Biol.* **34**(4), 425-446.

NIELSON, R. L. 1951. Effect of soil minerals on earthworms. *N.Z. J. Agric.* **83,** 433-435.

NIELSON, R. L. 1953. Recent research work. Earthworms. *N.Z. J. Agric.* **86,** 374.

NIJHAWAN, S. D. and KANWAR, J. S. 1952. Physic-chemical properties of earthworm castings and their effect on the productivity of soil. *Indian J. agric. Sci.* **22,** 357-373.

NYE, P. H. 1955. Some soil forming processes in the humid tropics. IV. The action of the soil fauna. *J. Soil Sci.* **6,** 73-83.

OGG, W. G. and NICOL, H. 1945. Balanced Manuring. *Scot. J. Agric.* **25**(2), 76-83.

PEELE, T. C. 1940. Microbial activity in relation to soil aggregation. *J. amer. Soc. Agron.* **32,** 204-212.

PEREDEL'SKY, A. A. 1957. [Foundations and objects of radioecology.] *Zh. obshch. Biol.* **18**(1), 17-30. [R.e.]

PEREDEL'SKY, A. A., PORIADKOVA, N. A., RODIONOVA, L. Z. *et al.* 1957. [The role of earthworms in the purification of soil from pollution with radio-active isotopes.] *Dokl. Akad. Nauk* **115**(4), 809-812. [R.]

POLIVKA, J. B. 1951. Effect of insecticides upon earthworm populations. *Ohio J. Sci.* **51,** 195-196.

PONOMAREVA, S. I. 1948. The rate of formation of calcite by earthworms in the soil. *Dokl. Akad. Nauk* **61,** 505-507.

PONOMAREVA, S. I. 1950. [The role of earthworms in the creation of a stable structure in ley rotations.] *Pochvovedenie*, 476-486. [R.]

PONOMAREVA, S. I. 1952. [The influence of the activity of earthworms in the mineralisation of plant residues.] *Pochvovedenie*, 727-732. [R.]

PONOMAREVA, S. I. 1953. [The effect of the activity of earthworms on the creation of a stable structure in a sod-podzolized soil.] *Trudy pochv. Inst. Dokuchaeva* **41,** 304-378. [R.]

POWERS, W. L. and BOLLEN, W. B. 1935. The chemical and biological nature of certain forest soils. *Soil Sci.* **40,** 321-329.

PRISYAZHNYUK, A. A. 1950. [Use of 666 for the control of chafer grubs.] *Agrobiologiya* No. 5, 141-142. [R.]

PUH, P. C. 1941. Beneficial influence of earthworms on some chemical properties of the soil. *Sci. Soc. China, Biol. Lab. Contrib., Zool. Ser.*, **15**, 147-155.

RAMANN, E. 1911. [Earthworms and microfauna in German forest soils. *Int. Mitt. Bodenk.* **1**, 138-164. [G.]

READ, R. A. and WALKER, W. C. 1950. Influence of Eastern redcedar on soil in Connecticut pine plantations. *J. For.* **48**, 337-339.

REYNOLDSON, T. B. 1955. Observations on the earthworms of North Wales. *Northw. Nat.* **3**, 291-304.

REYNOLDSON, T. B., O'CONNOR, F. B. and KELLY, W. A. 1955. Observations on the earthworms of Bardsey. *Bardsey Obs. Rep.*, pp 9.

RIBAUDCOURT, E. and COMBAULT, A. 1907. [The role of earthworms in agriculture.] *Bull. Soc. for. Belg.* [F.]

RICHARDSON, H. L. 1938. The nitrogen cycle in grassland soils: with special reference to the Rothamsted Park Grass Experiment. *J. agric. Sci.* **28**, 73-121.

RICHTER, G. 1953. [The action of insecticides on soil macrofauna. Quantitative investigations with treated and untreated forest soils.] *NachrBl. deutsch. PflSchD. Berlin* **8**, 61-72. [G.]

ROBERTSON, J. D. 1936. The function of the calciferous glands of earthworms. *J. exp. Biol.* **13**, 279-297.

RONDE, G. 1951. [Occurrence, population densities and species of earthworms in different soils under different cover types. I. Investigations in a forest enterprise of the Upper Bavarian Tertiary Uplands.] *Forstw. Cbl.* **70**(9), 521-552. [G.]

RONDE, G. 1953a. [Occurrence, population densities and species of earthworms in different soils under different cover types. II. Investigations in a forest enterprise of the Württemberg Alpine foothills.] *Forstw. Cbl.* **72**(1/2), 37-56. [G.]

RONDE, G. 1953b. [Occurrence, population densities and species of earthworms in different soils under different cover types. III. Investigations in the Inn-Chiemsee-Salzach morain district. IV. Investigations on the Munich pebble beds.] *Forstw. Cbl.* **72**(9/10), 286-301. [G.]

RONDE, G. 1954. [Occurrence, population densities and species of earthworms in different soils under different cover types. V. Investigations on Tertiary uplands in the Donau Moos. VI. Worm populations of a forest site in the course of the seasons.] *Forstw. Cbl.* **73**(3/4), 113-126. [G.]

RUSCHMANN, G. 1953. [Antibioses and symbioses of soil organisms and their significance in soil fertility. Earthworm symbioses and antibioses.] *Z. Acker- u. PflBau* **96**, 201-218. [G.]

RUSCHMANN, G. 1954. [Antibioses and symbioses of soil organisms and their significance in soil fertility. IV. Symbiotic and antibiotic earthworm actinomycetes.] *Z. Acker- u. PflBau* **97**, 101-114. [G.]

RUSSELL, E. J. 1910. The effect of earthworms on soil productiveness. *J. agric. Sci.* **3**, 246-257.

RUSSELL, E. J. 1950. Soil Conditions and Plant Growth. *Longman, London.* (8th edn. Revised by E. W. Russell.)

SALISBURY, E. J. 1923. The influence of earthworms on soil reaction and the stratification of undisturbed soils. *J. Linn. Soc.* (*Bot.*) **46**, 415-425.

SATCHELL, J. E. 1955a. Some aspects of earthworm ecology. *Soil Zoology* (*Proc. Nottingham Sch. agric. Sci.*), 180-199.

SATCHELL, J. E. 1955b. An electrical method of sampling earthworm populations. *Soil Zoology* (*Proc.Nottingham Sch. agric. Sci.*), 356-364.

SATCHELL, J. E. 1955c. *Allolobophora limicola*—an earthworm new to Britain. *Ann. Mag. nat. Hist.* Ser. 12, **8**, 224.

SATCHELL, J. E. 1955d. The effects of BHC, DDT and parathion on soil fauna. *Soils & Fert.* **18**, 279-285.

SAUSSEY, M. 1955. [Observations on the relations between the physico-chemical composition and its Lumbricid population.] *Arch. Zool. exp. gén.* **93**, 123-134. [F.]

SCHÜTZ, W. and FELBER, E. 1956. [What micro-organisms participate in the formation of soil aggregates in the gut of earthworms?] *Z. Acker- u. PflBau* **101**, 471-476. [G.]

SEARS, P. D. and EVANS, L. T. 1953. Pasture growth and soil fertility. III. The influence of red and white clovers, superphosphate, lime, and dung and urine on soil composition, and on earthworm and grass-grub populations. *N.Z. J. Sci. Tech.*, **35**(A), Suppl. 1, 42-52.

SHRIKHANDE, J. G. and PATHAK, A. N. 1951. A comparative study of the physico-chemical characters of the castings of different insects. *Indian J. agric. Sci.* **21**, 401-407.

SJÖRS, H. 1954. [Meadows in Grangärde Finnmark.] *Acta phytogeogr. Suec.* **34**, 1-135. [Sw.]

SLATER, C. S. and HOPP, H. 1947. Relation of fall protection to earthworm populations and soil physical conditions. *Soil Sci. Soc. Amer. Proc.* **12**, 508-511.

SMITH, R. L. 1957. An evaluation of conifer plantations as wildlife habitat. *Diss. Abstr.* **17**(3), 465-466.

SPANNAGEL, G. 1954. [Model experiment with earthworms on the subject of soil formation and increase of soil fertility.] *Z. PflErnähr. Düng.* **64**, 217-222. [G.]

STEBLER, F. G., THIELE, E., VOLKART, U., *et al.* 1904. [26th Report of the Swiss Seed Research Institute, Zurich. (Investigations on the influence of earthworms on the condition of turf).] *Landw. Jb. Schweiz*, 45-100. [G.]

STÖCKLI, A. 1928. [Studies on the influence of earthworms on the soil condition.] *Landw. Jb. Schweiz* **42**, 5-121. [G.]

STÖCKLI, A. 1949. [The influence of microflora and fauna on soil conditions.] *Z. PflErnähr. Düng.* **45**, 41-53. [G.]

SVENDSEN, J. A. 1955. Earthworm population studies: a comparison of sampling methods. *Nature Lond.* **175**, 864.

SVENDSEN, J. A. 1957a. The distribution of Lumbricidae in an area of Pennine moorland (Moor House Nature Reserve). *J. Anim. Ecol.* **26**, 411-421.

SVENDSEN, J. A. 1957b. The behaviour of Lumbricids under moorland conditions. *J. Anim. Ecol.* **26**, 423-439.

SWABY, R. J. 1949a. The influence of earthworms on soil aggregation. *J. Soil Sci.* **1**(2), 195-197.

SWABY, R. J. 1949b. The influence of humus on soil aggregation. *J. Soil Sci.* **1**(2), 182-194.

TEOTIA, S. P., DULEY, F. L. and MCCALLA, T. M. 1950. Effect of stubble mulching on number and activity of earthworms. *Neb. agric. Exp. Sta. Res. Bull.* **165**, 1-20.

TISCHLER, W. 1955. Effect of agricultural practice on the soil fauna. *Soil Zoology* (*Proc. Nottingham Sch. agric. Sci.*), 215-228.

TRACEY, M. V. 1951. Cellulase and chitinase of earthworms. *Nature Lond.* **167**, 776.

UHLEN, G. 1953. [Preliminary experiments with earthworms.] *LandbrHøgsk. Inst. Jordkultur Meld.* No. 37, 161-183. [N.e.]

WAKSMAN, S. A. and MARTIN, J. P. 1939. The conservation of the soil. *Science* **90**, 304-305.

WATERS, R. A. S. 1955. Numbers and weights of earthworms under a highly productive pasture. *N.Z. J. Sci. Tech.* **36**(A), 516-525.

WATKIN, B. R. 1954. The animal factor and levels of nitrogen. *J. brit. Grassl. Soc.* **9**, 35-46.

WATSON, M. R. and SMITH, R. H. 1956. The chemical composition of earthworm cuticle. *Biochem. J.* **64**(1). *Proc. biochem. Soc.*, p. 10.

WEBER, G. 1953. [The macrofauna of light and heavy arable soils and the effect on them of plant-protection substances.] *Z. PflErnähr. Düng.* **61**, 107-118. [G.]

WILCKE, D. E. VON. 1952. [On the "domestication" of the "soilution earthworm".] *Anz. Schädlingsk.* **25**, 107-109. [G.]

WILCKE, D. E. VON. 1953. [On the vertical distribution of the Lumbricidae in soil.] *Z. Morph. Ökol. Tiere* **41**, 372-385. [G.]

WILCKE, D. E. VON. 1955. [Critical observations and proposals on the quantitative analysis of earthworm populations in soil zoology studies.] *Z. PflErnähr. Düng.* **68**, 44-49. [G.]

WITTICH, W. 1952. [Our present knowledge about humus and the new approach to solving the raw-humus problem in forests.] *SchrReihe forstl. Fak. Göttingen* **4**, 1-106. [G.]

WITTICH, W. 1953. [Investigations on the course of decomposition of litter in ground with great earthworm activity.] *SchrReihe forstl. Fak. Göttingen* 9, 7-33. [G]

WOLLNY, E. 1890. [Investigations on the influence of earthworm activity on the fertility of soil.] *Forscharb. Geb. Agr.-phys.* **13,** 381-395. [G.]

WOLLNY, E. 1897. [The Decomposition of Organic Matter and the Formation of Humus.] *Heidelberg.* Pp. 480. [G.]

ZICSI, A. 1954. [The role of earthworms in the soil, as investigated by soil analyses, experiments and survey at the University in Gödöllö.] *Agrártud. Egyet. agron. Kar Kiadv.* 1(14), 1-20. [H.r.g.]